

NATURAL HYBRIDIZATION IN WESTERN GOOSEBERRIES
(*RIBES* SUBGENUS *GROSSULARIA*: GROSSULARIACEAE)

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ABSTRACT

We describe three cases of hybridization between species of *Ribes* in the Klamath Mountains of northern California and southern Oregon. Based on their intermediacy and reduced pollen viability, we identified putative hybrids between *R. lobbii* and *R. roezlii* var. *cruentum*, *R. binominatum* and *R. marshallii*, and *R. binominatum* and *R. lobbii*. The hybrids live in recently cleared forests, where logging created extensive areas suitable for seedling establishment. Even though they are partially fertile, backcrossing and interbreeding have not generated an extensive array of recombinant types. Judging from field observations and surveys of herbarium specimens, hybridization between these species of *Ribes* appears to be uncommon, and there is little evidence that introgression is blurring the distinctions between them.

Like members of many other woody genera, closely related species of *Ribes* are interfertile (Keep 1962) and presumably capable of hybridizing where sympatric. Numerous reports of spontaneous garden hybrids attest to this potential (Janczweski 1907, 1909, 1911, 1916). Not surprisingly, many botanists assume that hybridization is common in *Ribes*, as it is in other genera with comparable patterns of interspecific fertility (e.g., Grant 1981, p. 312). However, as yet there is little field evidence to support this view. We know of only three papers that describe wild *Ribes* hybrids. Two of these (Henry 1919, *R. lobbii* × *R. divaricatum*; Anderson, 1943, *R. bracteosum* × *R. laxiflorum*) are very brief accounts, based on the discovery of a single specimen. Sinnott (1985) discussed several possible cases of hybridization in his revision of section *Grossularia*, but he did not present detailed supporting evidence. At least some of the patterns he observed could be the result of divergent evolution. Clearly, the importance of natural hybridization in *Ribes* is not yet known.

In this paper we document three cases of natural hybridization between species of *Ribes* in the Klamath Mountains of northern California and southern Oregon. Based on their morphological intermediacy and reduced pollen fertility, we have identified hybrids between *R. lobbii* A. Gray and *R. roezlii* Regel var. *cruentum* (E. Greene) Rehder, *R. binominatum* Heller and *R. marshallii* E. Greene, and *R. binominatum* and *R. lobbii*.

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METHODS

The species. The four parental species are compared in Table 1 and Figures 1 and 2. All are members of subgenus *Grossularia* (P. Miller) Pers., and all have glabrous styles, unlike the species that comprise section *Grossularia* (Sinnott 1985). Otherwise, the relationships of the four species inter se are uncertain. *R. roezlii* is more closely related to other species with connivent, lanceolate anthers (like *R. menziesii* Pursh) than it is to *R. binominatum*, *R. lobbii*, or *R. marshallii* (Berger, 1924). Likewise, *R. binominatum* appears to be more closely allied to *R. watsonianum* Koehne and *R. tularense* (Coville) Fedde. Janczewski (1907) and Berger (1924) both regarded *R. lobbii* and *R. marshallii* as close relatives, although the two species differ in many respects, especially petal shape and fruit vestiture. In fact, *R. lobbii* strongly resembles *R. roezlii* in petal shape and flower color, and it is similar to *R. sericeum* Eastwood in other respects. The relationships of *R. marshallii* are least apparent; its distinctive deeply concave petals, and complete lack of glandular hairs, set it off sharply from other gooseberries. Keep (1962) did not attempt garden crosses involving the four parental species, so we do not know to what degree they are interfertile.

Study sites. We made our observations at five sites in northern California and southern Oregon (Appendix I). We chose three sites where *R. lobbii*, *R. roezlii*, and suspected hybrids occurred together. Morphometric data are presented for only one of these (Horse Mountain) because the patterns at all sites were similar. We studied hybridization between *R. binominatum* and *R. marshallii* and between *R. binominatum* and *R. lobbii* at a site in southern Oregon (Bigelow Lake). Additional hybrids between *R. binominatum* and *R. marshallii* were collected about 1 km away (Mt. Elijah) and included in the analysis. Voucher specimens are filed at HSC.

With the exception of Mt. Elijah, the sites were large disturbed areas in forests that had been completely logged 15 or more years ago. At Mt. Elijah, the suspected hybrids grew along a disturbed roadside adjacent to a relatively undisturbed forest. At all sites, the suspected hybrids were less common than the parental species. Hybrids and parents grew intermixed except at Bigelow Lake, where *R. marshallii* appeared to be restricted to shady sites in the understory of the forest adjacent to the cleared area.

Sampling and morphological analysis. At each site we collected several flowering branches from a sample of parental species and suspected hybrids. At all sites except Big Flat, the samples consisted of more than 90% of the flowering individuals present at the locality. At Big Flat, a random sample of plants was collected along three 50 m transects. Plants at Horse Mountain were marked so that mature

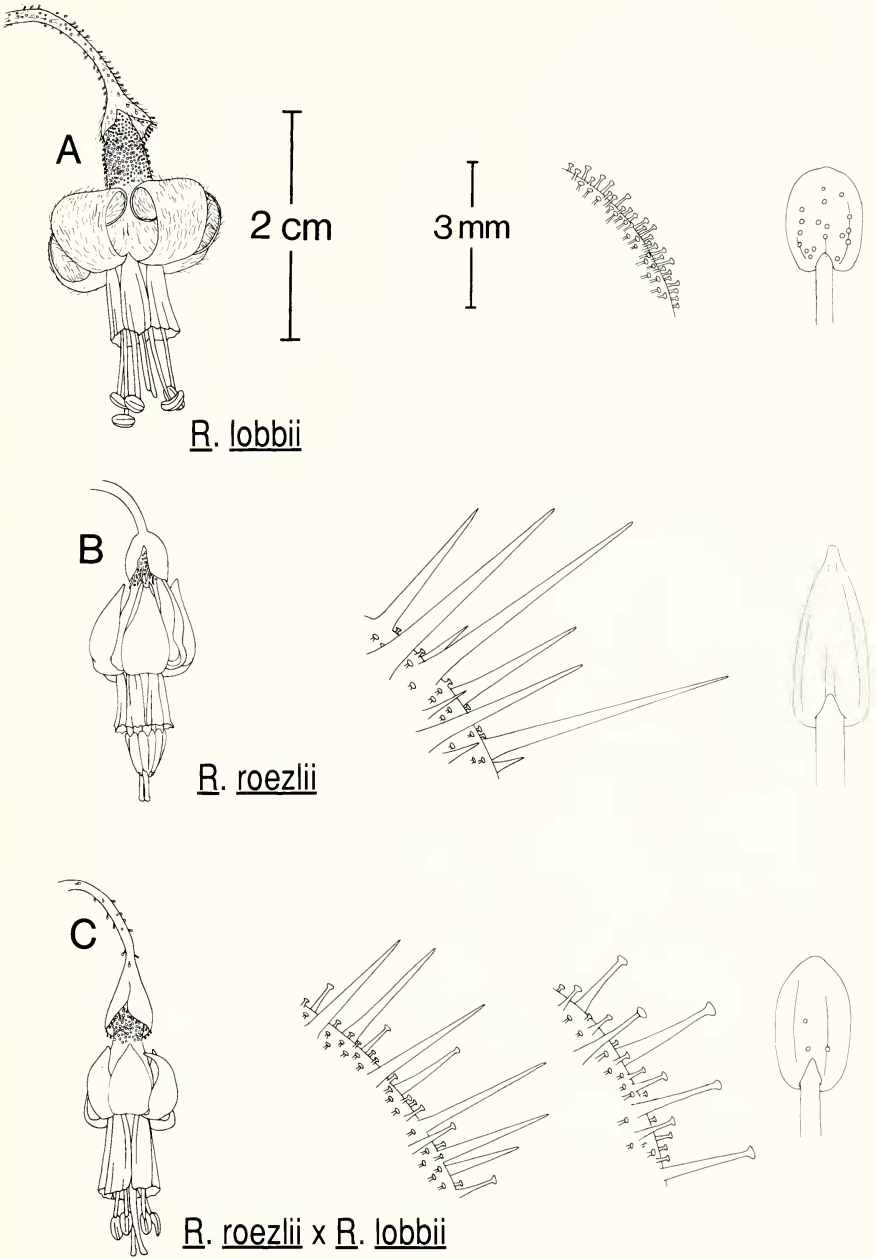


FIG. 1. Flowers, fruit surfaces, and anthers of *Ribes lobbii*, *R. roezlii* var. *cruentum*, and hybrid from the Horse Mountain population. A. *R. lobbii*. B. *R. roezlii* var. *cruentum*. C. Putative F₁ hybrid. Fruits of two individuals are shown.

TABLE 1. DIAGNOSTIC FEATURES AND DISTRIBUTIONS OF THE FOUR PARENTAL SPECIES.

Character	<i>R. roezlii</i> var. <i>cruentum</i>	<i>R. lobbiai</i>	<i>R. binominatum</i>	<i>R. marshallii</i>
Habit	upright shrub, >1 m, with rigid, divergent branches	upright shrub, >1 m, with rigid, divergent branches	low, trailing shrub, mostly <1 m, rooting along horizontal branches	low, \pm upright shrub, to about 1 m, spreading by arching shoots that root at tip
Glands on lower surface of short shoot leaves	absent	present	present	absent
Number of flowers/inflorescence	1 [2]	1-2 [3]	2-3 [1, 4]	1 [2]
Sepal color	crimson	crimson	green [red margin]	dark maroon
Petal				
Color	white [pink]	white [pink]	white [pink]	bright yellow
Shape	tubular (margins involute)	tubular (margins involute)	shallowly concave, rounded at apex	deeply concave, hooded at apex
Stamen exertion	just beyond petals, filaments barely visible	well beyond petals, filaments clearly visible	just beyond petals, filaments barely visible	well beyond petals, filaments clearly visible
Anther				
Color	purple	purple	white	yellow
Shape (after dehiscence)	lanceolate, with an apiculate apex	oblong, with a blunt or round apex	oblong, with rounded apex	oblong, with rounded apex
Position	connivent about the style	widely separated	widely separated	widely separated
Orientation (after dehiscence)	vertical, parallel to filaments	reflexed, perpendicular to filaments	vertical, parallel to filaments	vertical, parallel to filaments
Glands	absent	present	absent	absent
Fruit surface	non-glandular spines + short glandular hairs	even length glandular bristles	non-glandular spines + glandular hairs + non-glandular hairs	non-glandular spines + appressed non-glandular hairs
Elevational range	170-2000 m	1000-2300 m	900-2500 m	1500-2400 m

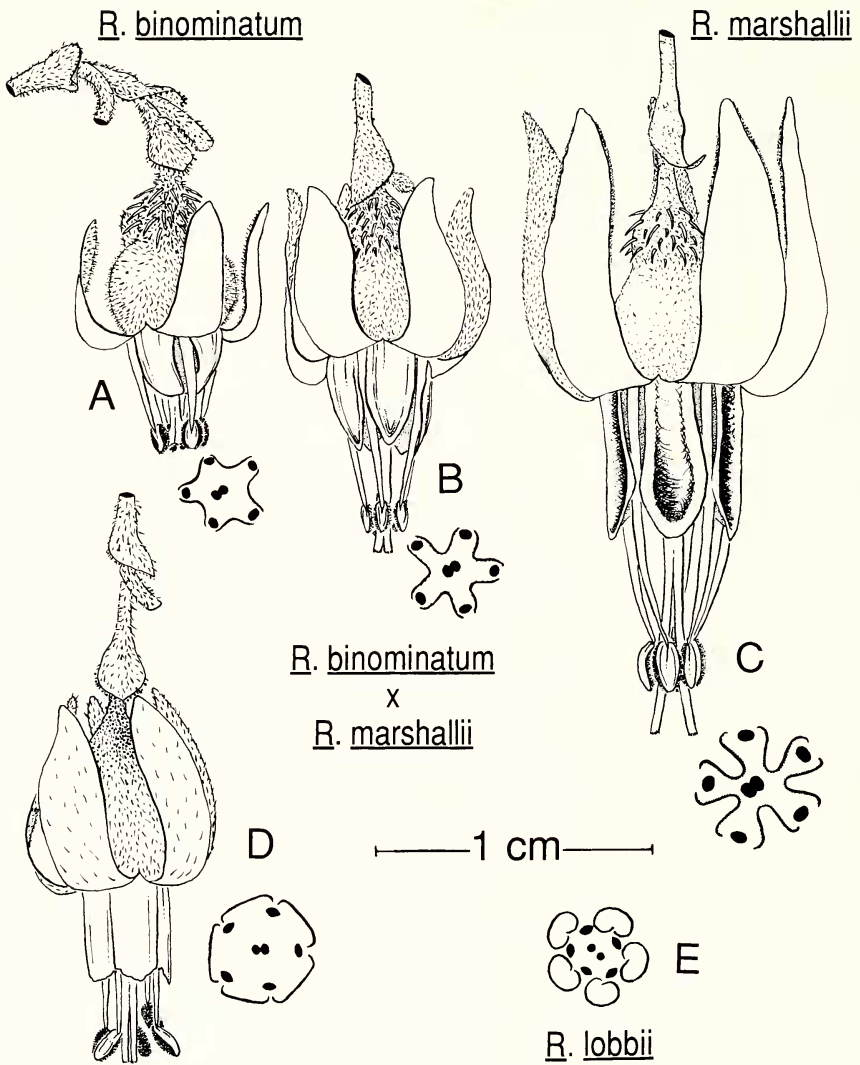
TABLE 1. CONTINUED.

Character	<i>R. roezlii</i> var. <i>cruentum</i>	<i>R. lobbii</i>	<i>R. binominatum</i>	<i>R. marshallii</i>
Distribution	Klamath, North Coast, and Cascade ranges, from Napa Co., CA to southern OR	Klamath, North Coast, and Cascade ranges, from northern CA to British Columbia	Klamath, North Coast, and Cascade ranges, from Lake Co. to southern OR	Klamath Mountains, northwest CA and southern OR

fruits could be collected later in the season. The fruits of the other groups could not be studied.

We used a series of univariate comparisons to test for overall intermediacy of the suspected hybrids and Anderson-style pictorialized scattergrams to look for evidence of hybridization beyond the F_1 generation. The characters used to study the three hybrid combinations are described below. In the case of *R. lobbii*, *R. roezlii*, and their hybrids, we made a single measurement or count per character per individual, except where noted, because preliminary studies showed relatively little within-plant variation (Cole, 1978). Otherwise, values are averages of three or more measurements per individual.

R. lobbii × *R. roezlii*. We scored 11 quantitative and two qualitative characters. Number of blade glands was indexed by counting the number of glands in a 5 mm × 5 mm area on the lower surface of the blade of a leaf taken from a short shoot. Degree of ovary exposure was calculated as the difference between bract length and the distance between the base of the pedicel and the top of the ovary. Number of bract margin glands was indexed by counting the glands along a 1 mm increment at the midpoint of the bract margin. Hypanthium length was measured from the top of the ovary to the insertion of petals and filaments. Petal length was measured from the hypanthium to the tip of the petal. Filament length is the length of the longest filament. Filament length difference is the difference between the length of the longest and shortest filament. Filament exertion is the difference between filament length and petal length. Anther length was measured from the tip of a dehiscent anther to the base of the lobes, if present. Number of anther glands is the average number of glands present on the abaxial surface of 10 anthers. Anther shape after dehiscence was scored as *R. roezlii*-like



R. binominatum x R. lobbii

FIG. 2. Flowers and flower cross-sections of *Ribes* from the Bigelow Lake population. Cross-sections show petals, styles, and filaments. A. *R. binominatum*. B. Putative F₁ hybrid between *R. binominatum* and *R. marshallii*. C. *R. marshallii*. D. Putative F₁ between *R. lobbii* and *R. binominatum*. E. *R. lobbii* (cross-section only).

(lanceolate, with a narrow apiculum), *R. lobbii*-like (oblong, with a rounded or truncate apex), or intermediate. Degree of style fusion is the ratio of the fused increment of the style to total style length. Fruit surface was scored subjectively as *R. roezlii*-like (long eglandular spines of varying length plus short glandular hairs), *R. lobbii*-like (glandular bristles of the same length), or intermediate. A synthetic character, degree of overall glandularity, was calculated for use in the scattergram analysis. This measure is the sum of the number of blade, bract margin, and anther glands. Plants with no glands were scored as *R. roezlii*-like, with >20 glands as *R. lobbii*-like, and with 1–20 glands as intermediate.

R. binominatum \times *R. marshallii* and *R. binominatum* \times *R. lobbii*. Petal length, filament length, filament exertion, and number of anther glands were scored as described above. Number of flowers per inflorescence is an average based on counts of 10 inflorescences per plant. In the scattergram analysis, plants with an average of ≤ 1.1 flowers per inflorescence were scored as *R. marshallii*-like, with >2 flowers as *R. binominatum*-like, and with 1.2–2 as intermediate. Degree of blade pubescence was scored as glabrous, densely pubescent, or intermediate. Sepal length was measured from the hypanthium to the tip of the sepal. Sepal color, petal color, and petal shape were scored subjectively as either a parental or intermediate state.

Pollen fertility. We estimated the relative fertility of the parental species and the suspected hybrids by comparing the percentage of pollen grains that stained in lactophenol blue. We scored 200 grains per plant from 10 plants in each of the three groups at Big Flat, and from five plants in each group at Bigelow Lake, except for *R. binominatum* \times *R. lobbii* ($n = 2$). Pairwise tests of significance (hybrid vs. parental species) were made using the non-parametric STP procedure (Sokal and Rohlf 1969) for the comparisons at Big Flat (see Cole 1978) and Mann-Whitney tests for the comparisons at Bigelow Lake, except for *R. binominatum* \times *R. lobbii*, where the sample size precluded testing.

RESULTS

Morphology. *R. lobbii* \times *R. roezlii*. The plants we identified as putative hybrids proved to be more-or-less intermediate between *R. lobbii* and *R. roezlii* in most respects. Mean values for all 11 quantitative variables lay between those of the two parental species, although in most cases their ranges overlapped substantially. Figure 3 shows comparisons for 10 of the 11 characters. With one exception (hypanthium length), all differences between the means of hybrids and parents were significant ($p < 0.05$, Dunn's nonparametric multiple comparison test, Zar 1984).

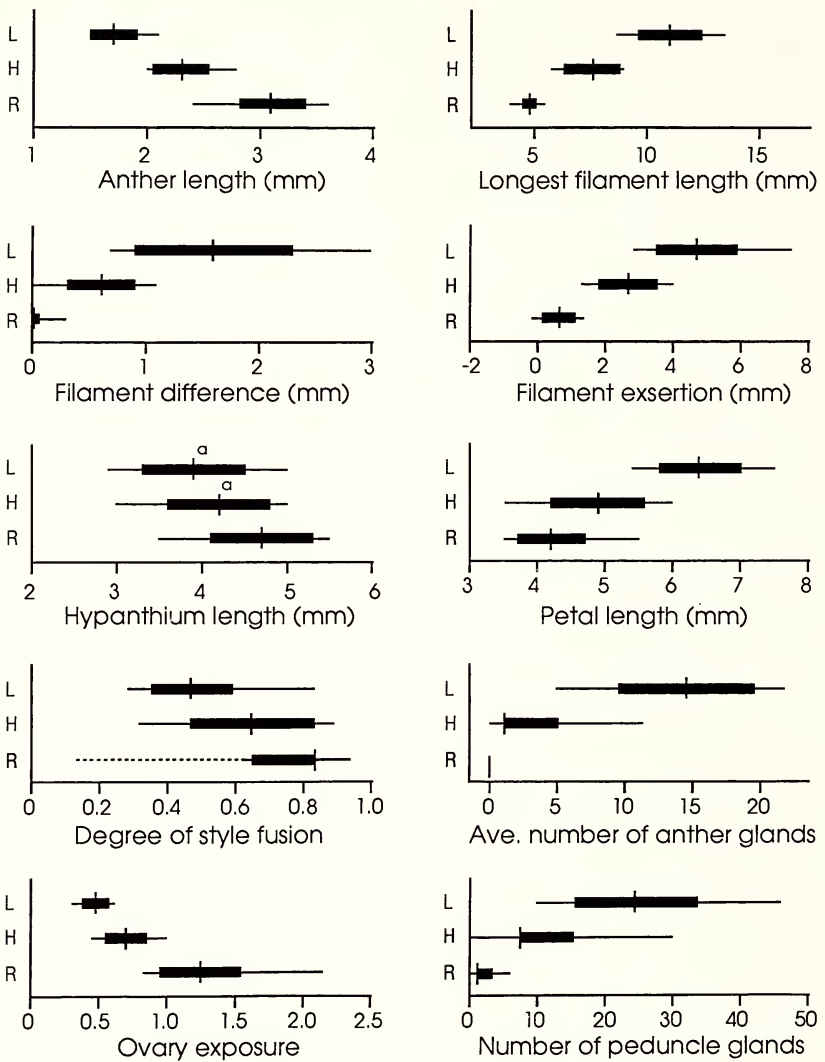


FIG. 3. Comparison of *R. lobbii* (L), *R. roezlii* (R), and putative hybrids (H) at the Horse Mountain population. Mean, SD, and range are shown for 10 reproductive characters. An extreme outlier for style fusion is shown with a dotted line. $n = 18$ for L, 25 for R, and 14 for $L \times R$. All pairwise comparisons of means are significant at the 0.05 level, except for the one indicated by the same lowercase letter.

Individuals are plotted as a function of anther and filament length on the scattergram shown in Figure 4. The symbols depict variation in fruit morphology, anther shape, and degree of overall glandularity. The scattergram shows a loose cluster of points between the two

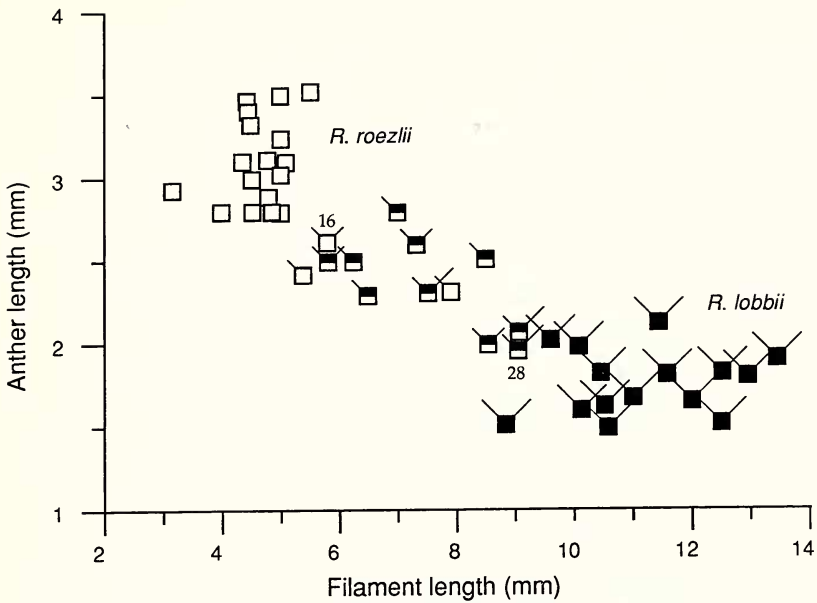


FIG. 4. Scattergram of plants at Horse Mountain. Box shading indicates anther shape (unshaded = *R. roezlii*-like, shaded = *R. lobbia*-like, half-shaded = intermediate). Arms represent degree of overall glandularity (right corner) and fruit surface (left corner). No arm = *R. roezlii*-like, full arm = *R. lobbia*-like, half-arm = intermediate. Numbered plants are discussed in the text.

species that corresponds to the putative hybrids. Most of the central plants are probably F_1 hybrids, although several are much less glandular than expected. A few plants resemble one or the other parent in some respects but have other characters that are intermediate. These may be the products of backcrossing. For example, plant 16 approaches *R. roezlii* in anther length, anther shape, and filament length but has intermediate fruits and glandularity. Plant 28 resembles *R. lobbia* in having long filaments, short anthers, and numerous glands, but is intermediate in anther shape and fruit morphology.

Hybrids can be distinguished from *R. roezlii* by their well-exserted filaments, the presence of at least a few glands on blades, bract margins, and/or anthers, anthers that do not form a tight cone around the style, and fruits with short spines, some or all of which are gland-tipped, depending on the individual (Fig. 1). They can be distinguished from *R. lobbia* by their subequal filaments, relatively long, narrow anthers that are not reflexed after dehiscence, and fruits with short spines in addition to shorter glandular bristles and hairs.

R. binominatum \times *R. marshallii*. The putative hybrids combine parental traits in an obviously intermediate fashion. Hybrids are not

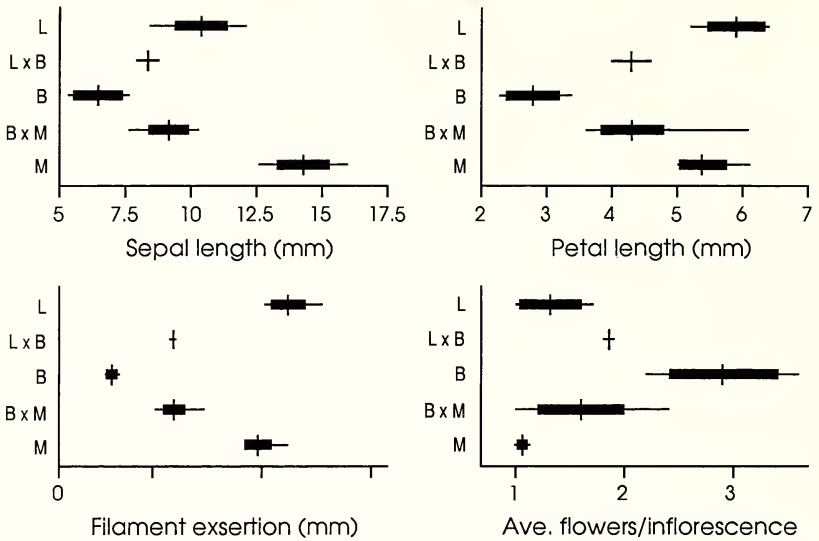


FIG. 5. Comparison of *R. binominatum* (B), *R. lobbii* (L), *R. marshallii* (M), and putative hybrids (H) at the Bigelow Lake and Mt. Elijah populations. Mean, SD, and range are shown for 4 floral traits. $n = 10$ for B, 10 for L, 9 for M, 21 for B \times M, and 2 for B \times L. All pairwise comparisons of means involving B, M, and B \times M are significant at the 0.05 level.

as low-growing as *R. binominatum*, but they have a scrambling habit, with more-or-less horizontal branches that root at the tip. Individuals can form tangled low brambles several meters in diameter that clamber over downed logs and stumps. Hybrids have moderately pubescent blades with a few glands on the lower surface. Their sepals and petals are pale maroon and pale yellow, respectively, the expected result of combining the light colors of the *R. binominatum* perianth with the intense colors of *R. marshallii*. The petals of hybrids are more strongly concave than those of *R. binominatum* but lack the hooded apex characteristic of *R. marshallii* (Fig. 2). Hybrid intermediacy in four additional characters is shown in Figure 5.

The scattergram (Fig. 6) confirms the intermediate character of the putative hybrids, which appear tightly grouped in the center of the graph. Three apparent hybrids resemble *R. binominatum* in sepal length and filament exertion, but otherwise the central plants have a uniform set of intermediate traits, consistent with the idea that they are F_1 's.

R. binominatum \times *R. lobbii*. We found two individuals at the Bigelow Lake site that appear to be F_1 hybrids between *R. binominatum* and *R. lobbii*. Both are upright shrubs less than 1 m tall. Their

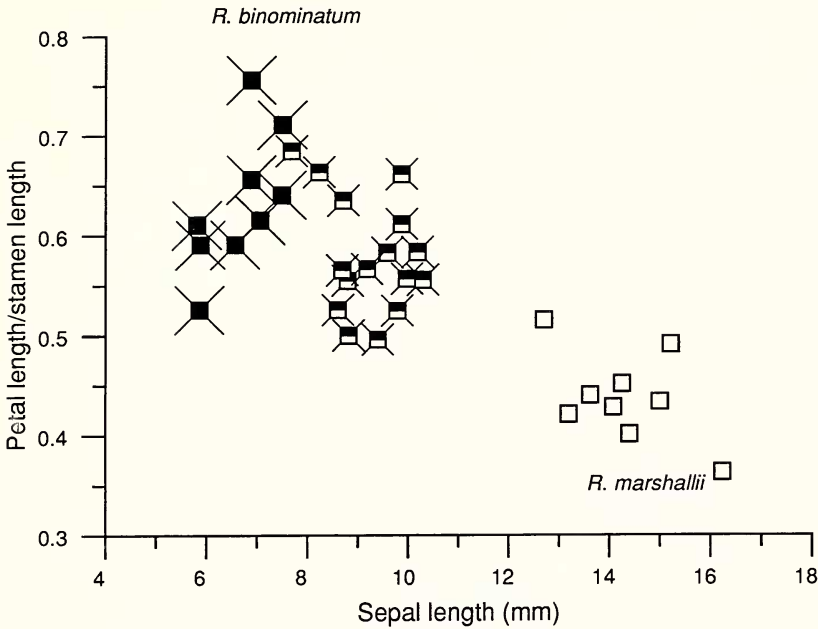


FIG. 6. Scattergram of plants of *R. binominatum*, *R. marshallii*, and putative hybrids from Bigelow Lake and Mt. Elijah. Box shading indicates degree of blade pubescence, and the arms show variation in petal color, petal shape, sepal color, and the average number of flowers/inflorescence. No arm = *R. marshallii*-like, full arm = *R. binominatum*-like, half-arm = intermediate.

flowers resemble those of *R. lobbii* but are smaller and have pale red (versus crimson) sepals and flat petals with the margins only involute. Anthers are tan, with a few glands on the abaxial surface, and are held at approximately a 45° angle to the filament. The two plants are also intermediate in sepal and petal length, degree of filament exertion, and in the number of flowers per inflorescence (Fig. 5).

Not surprisingly, these hybrids resemble those between *R. binominatum* and *R. marshallii* (Fig. 2) but can be recognized easily by their sepal color (pale red versus pale maroon), petal color (white to pink versus pale yellow), petal morphology (flat with involute margins versus concave), anther color (tan versus pale yellow), and the presence of a few anther glands.

Pollen fertility. In all three cases, hybrids had a lower percentage of stained and presumably viable grains than the parental species. At Big Flat, average values were: *R. lobbii* (95%), *R. lobbii* × *R. roezlii* (85%), *R. roezlii* (97%). At Bigelow Lake, averages were: *R. marshallii* (93%), *R. binominatum* × *R. marshallii* (68%), *R. bi-*

nominatum (91%), *R. binominatum* × *R. lobbii* (51%), *R. lobbii* (82%). The small sample size precluded testing the difference between *R. binominatum* × *R. lobbii* and its parents, but the differences between the other two hybrids and their parents were significant ($p < 0.05$).

DISCUSSION

Morphological intermediacy and reduced pollen stainability support the idea that *R. lobbii* and *R. roezlii*, *R. binominatum* and *R. marshallii*, and *R. binominatum* and *R. lobbii* hybridize in the Klamath Mountains. Other evidence, however, suggests that hybridization between these species is infrequent and localized, and that it has had little impact on the integrity of the species.

Our surveys of herbarium collections from northern California and southern Oregon, together with several years of field observation, indicate that hybridization involving the four species of gooseberries is uncommon. To date, the only hybrids between *R. binominatum* and *R. lobbii* we have found are the two plants at our Bigelow Lake study site. Hybrids between *R. binominatum* and *R. marshallii* are common at the same site, but currently we know of only two other places where they occur. Hybridization between *R. lobbii* and *R. roezlii* appears to be more common, which is not surprising considering the relatively greater zone of contact between the two species. Nevertheless, even though the species are commonly sympatric, we know of fewer than 10 localities where hybrids occur, although additional ones are likely to be discovered in the future.

More important than frequency of occurrence to an understanding of the evolutionary significance of hybridization is the issue of whether interbreeding goes beyond the F_1 generation. We believe that it seldom does in this group of gooseberries. With few exceptions, plants in the field were readily identifiable as one of the parental taxa or as putative F_1 hybrids. Our scattergrams confirm this initial impression that mixed populations consisted of distinct groups, with little or no intergradation between them. The graphs show little evidence of the kind of recombination of parental traits that would be expected as the result of backcrossing or interbreeding among hybrids. A few hybrid-type individuals at Horse Mountain appear to vary in the direction of either *R. lobbii* or *R. roezlii*, but these are in the minority. In most cases, hybridization between these species appears to stop at the F_1 stage.

Even with limited backcrossing, genes from one species may be incorporated into another via introgression. Our preliminary analyses of allopatric populations of the four parental species reveal little, if any, gene transfer between the species. The only possible exceptions are a few populations of *R. roezlii* that appear to vary in the

direction of *R. lobbii* in one or another respect. For example, in some populations of *R. roezlii*, the filaments are exerted more strongly than is usual for the species, suggesting the influence of *R. lobbii*, which has strongly exerted filaments. In other cases, glands are present on the peduncles (normally glabrous) or the bracts cover the ovary less completely than the norm for the species. However, since only a single trait is involved in these cases, we believe that coincidental within-species variation is a more parsimonious explanation than introgressive transfer of genes from *R. lobbii*.

Several factors may limit hybridization in this group of *Ribes*. The relatively high pollen fertility of the suspected F_1 hybrids suggests that the species are interfertile, but since garden crosses have not been made, there is a possibility that some form of internal reproductive barrier (e.g., partial hybrid inviability, hybrid breakdown) limits hybridization. Several external mechanisms may also operate. Even though their ranges overlap in the Klamath Mountains, habitat specialization partially isolates the four species. For example, *R. roezlii* typically occurs at lower elevations than the other three species, in somewhat drier sites. In contrast, *R. marshallii* is restricted to mesic forests and meadows above 1500 m. Peak flowering is earlier for *R. roezlii* than for *R. lobbii* (Cole 1978), but the flowering periods of all four species overlap substantially, which should provide ample opportunity for hybridization where they are sympatric. The flowers of *R. lobbii* and *R. roezlii* are very similar, and not surprisingly, they are visited by the same set of pollinators (Cole 1978). By contrast, the flowers of *R. binominatum* and *R. marshallii* differ in many respects, suggesting that interspecific pollen transfer might be limited by mechanical or ethological factors (sensu Grant 1981). However, the abundance of F_1 hybrids between these two divergent species at Bigelow Lake indicates that floral isolation may be relatively unimportant in *Ribes* in general. Finally, the availability of suitable sites for establishment of hybrid seedlings may play an important role in determining the frequency and extent of hybridization. Hybrids are abundant only at localities where logging has created extensive open areas (Cole 1978). Large scale disturbance presumably provides ample room for establishment of parental species and enough time for recruitment of F_1 hybrid progeny before conditions become less favorable for seedling growth because of regeneration. At sites like Horse Mountain and Bigelow Lake, where plants of the parental species and F_1 hybrids are common, a dense herb layer probably prevents seedling establishment, which may help explain why backcrossing has not generated hybrid swarms.

Hybridization between interfertile species can result in the production of true-breeding homoploid derivatives that combine the traits of the species in "kaleidoscopic fashion" (Raven 1976, p. 295). This mode of evolution, termed hybrid speciation (Grant 1981), has

been a dominant factor in the diversification of several groups of woody and herbaceous perennials in California (Raven and Axelrod 1978). Has hybridization played a comparable role in the evolution of *Ribes*, a genus with nearly one-fourth of its species native to the state? Sinnott (1985, p. 218), believed that "hybridization and reticulate evolution dominate the genus." Raven and Axelrod (1978, p. 79) included *Ribes* in a list of genera having "patterns suggestive of reticulate evolution." In contrast, our view is that the importance of hybridization in the genus is still poorly understood. Compared to other groups of woody plants with the "*Ceanothus* pattern" of species interfertility (Grant 1981; e.g., *Arctostaphylos*, *Ceanothus*, *Quercus*, and *Pinus*), the number of published records of hybridization in *Ribes* is surprisingly meagre. This apparent difference is intriguing, but at present our knowledge is too limited to determine whether it is simply an artifact of poor field sampling or is a real distinction requiring an explanation. Additional garden work is needed to determine the degree of interfertility of related species. Field studies are needed to establish how often interfertile species occur together and how often (and to what degree) they hybridize.

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APPENDIX I.

STUDY SITES

R. lobbii, *R. roezlii*, *R. lobbii* × *R. roezlii*

BIG FLAT. California: Trinity Co., Shasta-Trinity National Forest, T38N, R9W, S31, on steep slope above Coffee Creek Rd, in logged white fir forest, 1570 m.

BUCK PEAK. Oregon: Josephine Co., Siskiyou National Forest, T40S, R6W, S3, below weather station, near the end of Rd 067, 0.9 mi from Rd 4613, logged white fir forest, 1700 m.

HORSE MOUNTAIN. California: Humboldt Co., Six Rivers National Forest, T6N, R4E, S29, on both sides of Titlow Rd, logged white fir forest, 1300 m.

R. binominatum, *R. lobbii*, *R. marshallii*, *R. binominatum* × *R. marshallii*,
R. binominatum × *R. lobbii*

BIGELOW LAKE. Oregon: Josephine Co., Siskiyou National Forest, T40S, R6W, S11, SE of intersection of Rds 070 and 079, approximately 1 mi NE of Oregon Natl. Monument, logged white fir forest, 1700 m.

R. binominatum × *R. marshallii*

MT. ELIJAH. Oregon: Josephine Co., Siskiyou National Forest, T40S, R6W, S22, north side of Rd 048, approximately 0.75 mi S of Oregon Caves Natl. Monument, disturbed roadside through unlogged white fir forest, 1730 m.